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Comparison of growth, relative abundance, and diet of three sympatric *Hemiandrus* ground wētā (Orthoptera, Anostostomatidae) in a New Zealand Forest

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Abstract

Ecology is an essential discipline for understanding the biology and behavior of organisms. This study increased knowledge of three sympatric species of ground wētā (*Hemiandrus* spp.). *Hemiandrus* ground wētā are nocturnal Ensifera that live in burrows during the day, and for these reasons, there is limited knowledge of their activity, development, and diet. We examined the diet of *Hemiandrus electra*, *Hemiandrus* 'disparalis', and *Hemiandrus nox* by examining the crop contents of specimens caught in malaise traps set in a native forest (St Arnaud) over seven months during two spring-summer-autumn seasons (2004/2005 and 2005/2006). The three species investigated varied in the plant and invertebrate fragment proportions in their diets. *Hemiandrus electra* and *H.* 'disparalis' were predominantly herbivores, while *H. nox* was primarily carnivorous, although plant matter constituted 20% of its diet. We identified the species and sex of 966 *Hemiandrus* wētā that were intercepted by the same malaise traps. Our results showed that *H. electra* was the most abundant species, with 701 individuals, while 157 and 109 were identified as *H.* 'disparalis' and *H. nox*, respectively. Surprisingly, the species with maternal care (*H. electra*) was the only one of the three sympatric *Hemiandrus* to have an even sex ratio; for the other two species, more males were caught in the traps. Using hind leg dimensions, we categorized each female *H. electra* specimen using naïve Gaussian mixture model clustering, which identified five size clusters (putatively corresponding to instars). Based on the month of collection and the growth category, we observed no seasonality in the development of this species of ground wētā, as almost all instars were found in each month of the sampling period. This study found no evidence that these nocturnal forest species synchronize their growth or reproduction with seasons.

Keywords

H. 'disparalis' morphometrics, *H. electra*, *H. nox*, natural habitats, seasonality, sex, and species abundance

Introduction

In New Zealand, 19 described species of flightless Orthoptera are in the genus *Hemiandrus* Ander, 1938 (Anostostomatidae). All are active at night, using burrows in the soil during the day to hide from predators, from where their common name, ground wētā, is derived. There is limited knowledge of wētā ecology in relation to activity, growth and development, and diet because of the insect's nocturnal behavior, but diet is known to vary within the Anostostomatidae family in New Zealand and elsewhere. At the genus level, *Hemiandrus* in New Zealand are mostly omnivores (Wahid 1979, Butts 1983, Van Wyngaarden 1995), but where data are available, there is evidence that individual species differ in diet. For example, *H. maculifrons* (Walker 1869) has been found to be primarily carnivorous (Cary 1983), while *H. maia* Taylor Smith, Morgan-Richards, Trewick 2013 has been observed to consume fruit, invertebrates, and seeds (Taylor Smith et al. 2013). Similarly, diet varies in the related genus of endemic *Hemideina* White 1846 tree wētā. *Hemideina maori* (Pictet & Saussure, 1891) feeds on invertebrates, plants, and lichen (Wilson and Jamieson 2005), while *Hemideina thoracica* White 1846 is primarily herbivorous (Wehi and Hicks 2010, Brown 2013). It has been concluded that *H. crassidens* (Blanchard 1851) is opportunistic in dietary choice, although plants make up a major part of the food of this species (Griffin et al. 2011, Wyman et al. 2011, Dewhurst 2012). *Deinacrida* (White 1842) (giant wētā), such as *D. rugosa* (Buller 1871), are primarily herbivores (Mcintyre 2001), but the New Zealand tusked wētā *Motuweta riparia* (Johns 1997) is predatory (Gibbs 2002, Trewick pers. obs.). Overseas, the South African species *Libanasa vittatus* (Kirby 1899) is considered omnivorous but can be predatory (Toms 2001), and the diet of Australian Anostostomatidae spans invertebrates and

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fungi (Monteith and Field 2001). Variations in the feeding behavior of wētā species occupying the same environment could be evidence of resource partitioning, a strategy that reduces competition for limited resources. An equilibrium is unlikely when more than one species share the same resources, and competitive exclusion is thought to eventually lead to either the extinction of all but one species or to resource partitioning (Vandermeer et al. 2002). Thus, sympatric species may coexist using different resources (Agrawal and Klein 2000, Eubanks and Denno 2000, Kaplan and Denno 2007). Diet is often linked to relative abundance, with predatory species often occurring at lower densities than related herbivores in the same ecosystem (Turney et al. 2018).

Differences in diet due to sex and developmental stage have been observed in *Hemiandrus* ground wētā. Studies of *Hemiandrus celeano* Trewick, Taylor-Smith, Morgan-Richards 2020 showed diet differences between the sexes (Wahid 1979), while *H. subantarcticus* (Salmon 1950) differed among age classes (Butts 1983). However, neither *H. maculifrons* nor the undescribed *Hemiandrus* species collected from Tekapo showed sex or size variations in their diet (Cary 1983, Van Wyngaarden 1995). Research gaps remain regarding what determines diet variation in Anostostomatidae.

In contrast to diet, reproduction and seasonality have been well studied in the Anostostomatidae family (Field and Jarman 2001, Gwynne 2004, Wehi et al. 2012). Current knowledge of *Hemiandrus* ground wētā reproduction suggests that all species have overlapping generations with mating and egg laying between January and March (summer, autumn) (Gwynne 2004), although there is the possibility of females laying eggs in other months (Nboyine et al. 2018). Most arthropods show seasonal variation in reproduction, which may be controlled by different factors (Ribeiro and Freitas 2011). For example, optimum temperature and humidity favor some species to mate and oviposit, and some insects may avoid emerging when parasitoids (Barbosa et al. 2007) or predation threaten their survival (Torres-Vila and Rodríguez-Molina 2002). One aspect that could affect seasonal variation in insects is the availability of vital resources that should be in synchrony with the larval or adult phase, and fewer of these resources could compromise the fitness of organisms (Torres-Vila and Rodríguez-Molina 2002, Kursar et al. 2006). In some forests, resources could be available all year round (Cary 1983), but the quality of these resources may vary (Lawrence et al. 1997). For instance, when new leaves emerge in forests, this could mean that the leaves are highly nutritious, with higher nitrogen, sugars, and amino acid contents than older leaves (Hamer et al. 2006). Therefore, such seasonal resource availability could affect mating or oviposition, and thus influence insect seasonality.

This study gleaned new ecological information about three endemic ground wētā species that co-occur in the same temperate rain forest: *Hemiandrus electra* Taylor Smith, Morgan-Richards & Trewick, 2013, *H. nox* Taylor-Smith, Trewick & Morgan-Richards, 2016, and an undescribed *Hemiandrus* species (Johns 2001). We addressed four main questions: 1) What are the main constituents of their diet? We expected all three wētā species to be omnivores, but the relative proportions of plant and animal matter might differ among species and sexes. As some *Hemiandrus* species are pests of economic importance in New Zealand (Nboyine et al. 2016), understanding the natural diet of related taxa could affect management decisions. 2) What are the relative abundances and sex ratios of these three sympatric species based on intercept trapping? Some *Hemiandrus* species show maternal care, and females are less active when attending to eggs and nymphs within soil burrows (Gwynne 2004). We expected that *H. electra* would have fewer active adult females than males, compared with the other two *Hemiandrus* species. 3) What is the size distribution of the common *Hemiandrus* species caught in malaise traps? Are these species univoltine or multivoltine, as are other members of this insect family (Godfrey et al. 2023)?

Materials and methods

Study site.—The three species of *Hemiandrus* were sampled as bycatch in a long-running *Vespula* wasp management program in Rotoiti Mainland Island near St Arnaud South Island, New Zealand (-41°53'59.99"S, 172°51'59.99"E) (Paton et al. 2007). Groups of malaise traps were set in the mature temperate native forest dominated by evergreen beech (*Fuscospora*) species. Each malaise trap was positioned at ground level and fitted with glycol and detergent collection bottles to preserve invertebrates that climbed or flew to the apex of the trap. Traps were cleared weekly, and samples were sorted and transferred to 75–99% ethanol for storage. *Hemiandrus* wētā for the present study came from traps operating from November to May in 2004/2005 and 2005/2006 at two locations referred to as Lake Head Track (6 traps) and Rotoiti (20 traps) (Fig. 1). Weekly samples at each location were pooled by month to maximize the representation of taxa and size classes.

Specimen identification.—All malaise traps intercepted individuals of all three *Hemiandrus* species. Each wētā specimen was identified to species using reproductive and other morphological traits (Fig. 2). In short, adult *H. nox* females have dark, patched, strongly curved, long ovipositors in proportion to body length, and this species is sister to *H. maculifrons* (Taylor-Smith et al. 2016), which has been studied in some detail as the synonym *Zealandosandrus gracilis* (Cary 1981). Male *H. nox* have a short sub-genital plate with a narrow apex with a U-shaped distal margin that may extend beyond the styles (Taylor-Smith et al. 2016, Trewick et al. 2021). Adult *H. electra* females have moderately short ovipositors, and this species shows maternal care, as also seen in *Hemiandrus bilobatus* Ander, 1938. Male *H. electra* have blunt cerci, and the subgenital plate is slightly concave at the margins with pointed dark styli (Taylor Smith et al. 2013). The third species is undescribed but included in a list of possible species by the informal 'tag' name *H.* 'disparalis' (Johns 2001) and is a genetically distinct lineage (Pratt et al. 2008). Adult *H.* 'disparalis' females have a long ovipositor. Categorising young nymphs into species level using only their reproductive traits was challenging. Thus, two further morphological characteristics were used (Fig. 2). The hairs on the maxillary palps can distinguish *H. nox* from the other two species (Johns 2001), and the presence or absence of a prolateral spine on the hind femur can distinguish *H. electra* from *H.* 'disparalis' (Fig. 2).

Diet of three sympatric ground wētā species.—We targeted the crop content, not the midgut and hindgut, because food passes through the proventricular and is partially digested. Therefore, it is difficult to identify food categories from these sections (Cary 1983). Sixty-six adult wētā specimens (11 females and 11 males of each species) were randomly selected. The crop membrane was cut from each wētā using fine tweezers; care was taken to remove any broken membrane and fat. The crop contents were placed in a beaker with household bleach (~5% sodium hypochlorite) for two minutes, then rinsed with running water for two minutes in a 70-micron (uM) nylon cell strainer (Falcon brand). The collected crop content of one individual was mounted on a glass slide and stained using a frass-cuticle stain containing basic fuchsin.

Slides were examined under an Olympus SZX7 stereomicroscope (Olympus Corporation, Tokyo, Japan). Each slide was systematically scanned, and every fragment of food that could be identified was recorded as either plant (e.g., phloem vessels, grass cells, leaf cuticle) or invertebrate fragments (insect exoskeleton, chitin, cuticle, antenna, insect leg, mandible). Fragments not identifiable as plant or invertebrate fragments were considered uncommon and ignored. We did not try to further analyze the diet variation between the different months because no diet differences were visible during slide scanning. The minimum number of food fragments identified was 19, and the maximum was 81. From this, the mean proportion of the two food types eaten was calculated for each wētā and compared between the sexes and species. Images of the crop content remains were taken using an Olympus SZX7 stereomicroscope with an Olympus SC100 image capture (Olympus Corporation, Tokyo, Japan).

Body measurements and sex ratios.—A total of 966 insect specimens of the three wētā species caught from the malaise traps were used for body measurements and sex ratio quantification. To evaluate the relative abundance of males and females of each species, we used the morphological and sex categorization indicated above. An Olympus SZX7 Zoom Stereomicroscope with an attached SC100 digital camera image capture and Olympus CellSens Dimensions v1.6 software (Olympus Corporation Tokyo, Japan) was used to measure specimens. The right hind leg was removed from each wētā specimen, and the following items were measured: hind femur length (femur length), hind femur width at widest point (femur width), and tibia length (Fig. 3). These metrics provide a good guide of body size in hemimetabolous insects such as wētā (Bulgarella et al. 2014) and grasshoppers (Meza-Joya et al. 2022) and form the basis for analysis of insect size trends (Horne et al. 2018, Meza-Joya et al. 2022).

Data analysis for diets of three sympatric ground wētā species.—Data were analyzed using R v4.0.2 (R Core Team 2023) with the R package multcomp, and graphs were generated using ggplot2 (Wickham 2016). We used the linear model (lm function with factors: species, sex, diet type (plant or invertebrate), and possible interactions). Residual plots and Shapiro–Wilk normality tests were used to confirm that the model assumptions were not violated. Significant differences were determined using Tukey's HSD test at $p < 0.05$.

Data analysis for body size clusters.—For each of the three species, a summary of statistics was generated using R v4.0.2 (R Core Team 2023). Body size distribution was analyzed separately for the three species because of the differences in body size. For example, *H.* 'disparalis' is larger than the other two species, while *H. nox* is the smallest. Additionally, males and females were analyzed separately because females tend to be larger than males. Cluster classification analysis of body size measurements was conducted for only the species with a large sample size (*H. electra*; n = 701), allowing males and females to be analyzed separately. Gaussian mixture

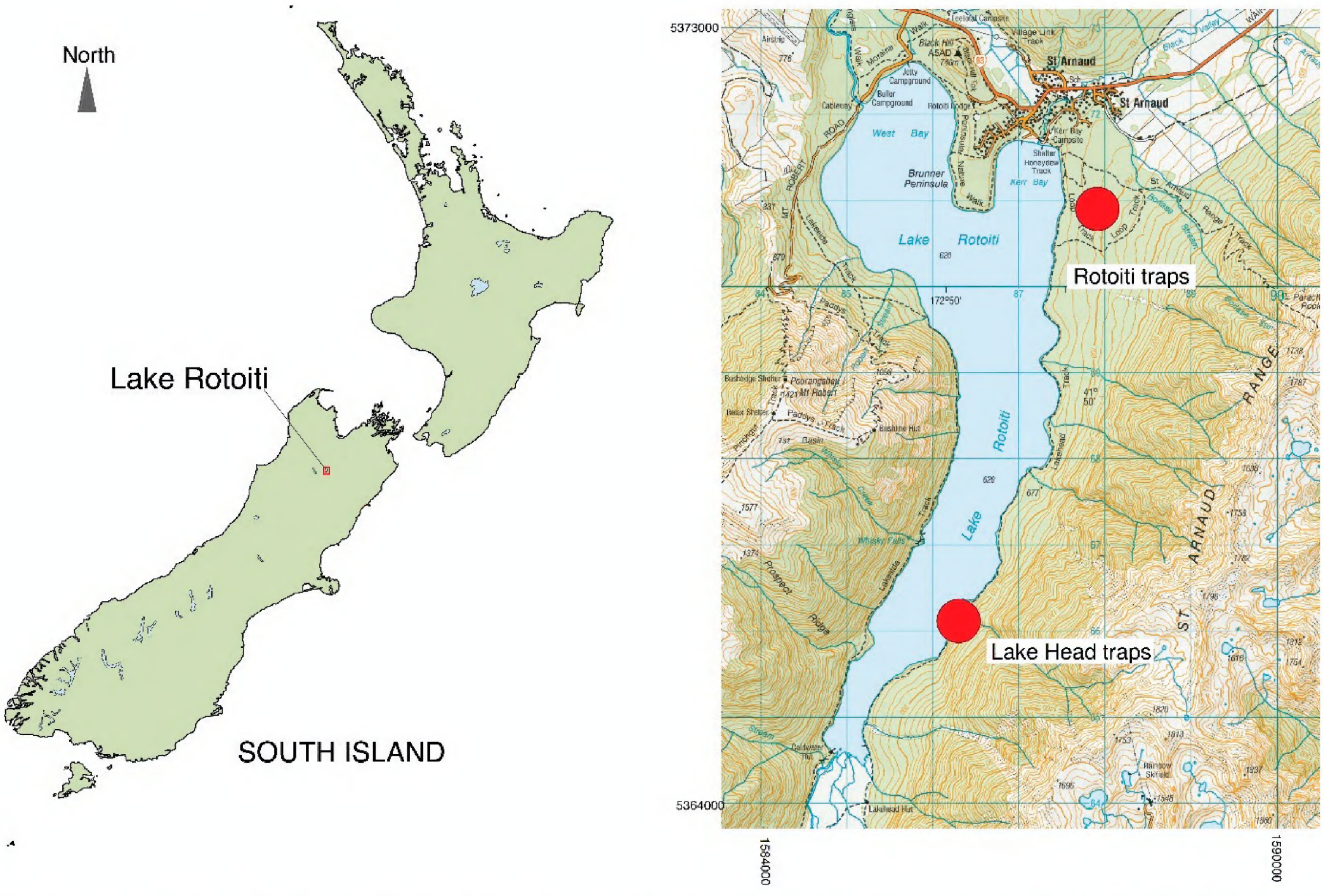

Fig. 1. Location of two malaise trap sites east of Lake Rotoiti, South Island, New Zealand, in which samples of three species of *Hemiandrus* ground wētā were collected. New Zealand Grid coordinates are shown on contour map (www.topomap.con.nz).

models were used to impartially examine size distributions of femur length, femur width, and tibia length variation to find the optimal number of groups (using R package MCLUST). MCLUST is a model-based clustering tool that groups data with similar properties and automatically determines optimal cluster numbers in the analyzed data without having *a priori* labels (Fraley and Raftery 2002). Bayesian information criteria (BIC) was used to determine the optimal number of clusters. Scales R package was used to normalize the data because the data contained variation in specimen abundance, and this was to ensure that each measurement contributed equally to the clustering process. Cluster data were generated in R and summarized with stacked bars plots to illustrate the numbers of individuals in each cluster of each size caught per month using Microsoft Excel®.

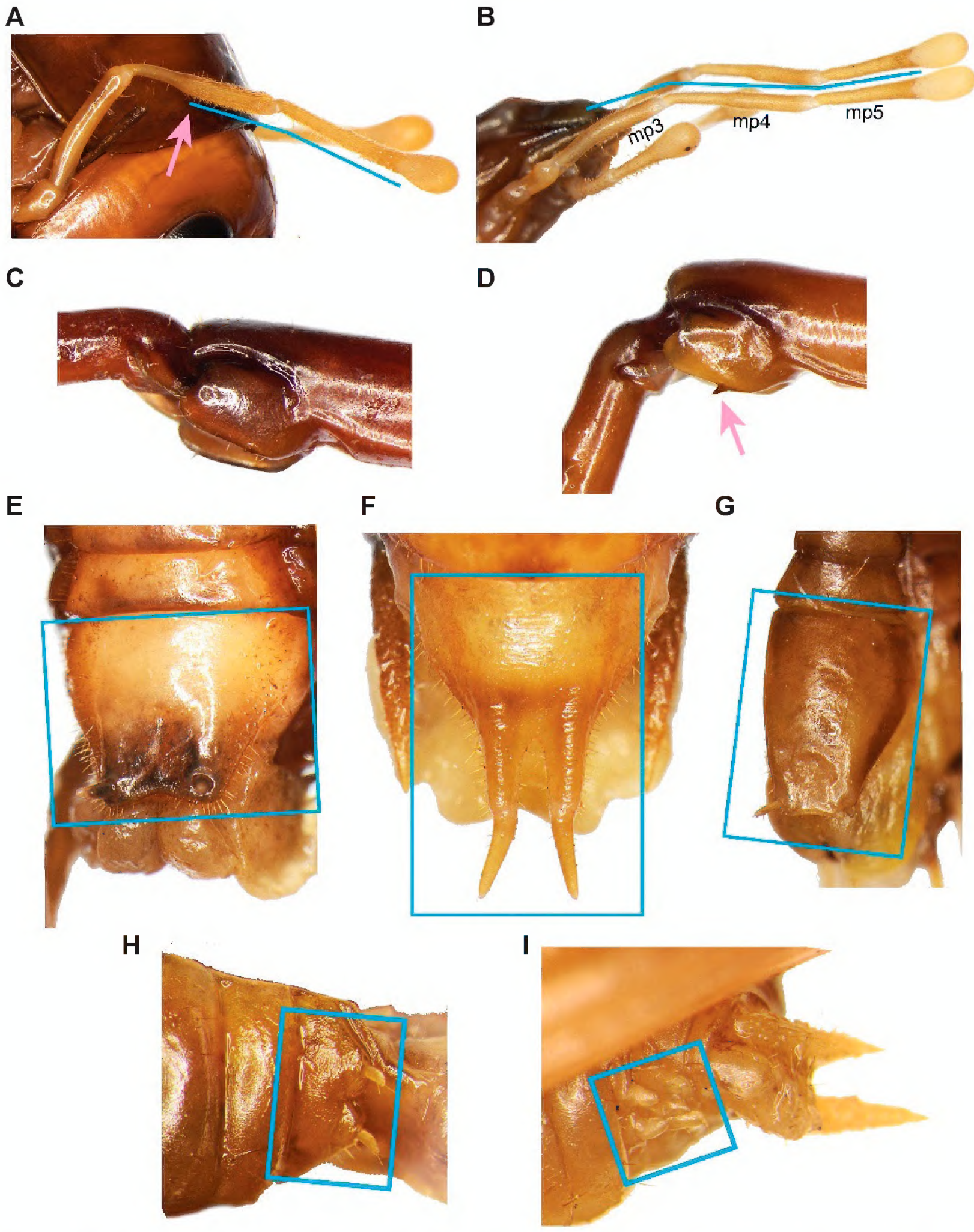

Fig. 2. Preserved ground wētā specimens from malaise traps deployed in St Arnaud Forest, New Zealand (-41°53'59.99"S, 172°51'59.99"E) were identified using morphological traits: **A.** *Hemiandrus electra* and *H.* 'disparalis' have fine hairs on segments of maxillary palp 5 (mp5) and part of (mp4). **B.** Pilosity on maxillary palps extends to mp3 in *H. nox*. **C.** *H. electra* has few or no prolateral apical spines on the hind femur. **D.** *H.* 'disparalis' has a stout spine apical spine on the hind femur. **E.** Male *H. electra* have a short, stout subgenital plate with shallow posterior dip and widely spaced short styli. **F.** Male *H.* 'disparalis' have a long, forked subgenital plate with long styli. **G.** Male *H. nox* have a relatively long, narrow, blunt subgenital plate with short styli. **H–I.** The sex of all instars can be determined by the subgenital plate, with two styli in males (**H**) and four incipient ovipositor valves in females (**I**).

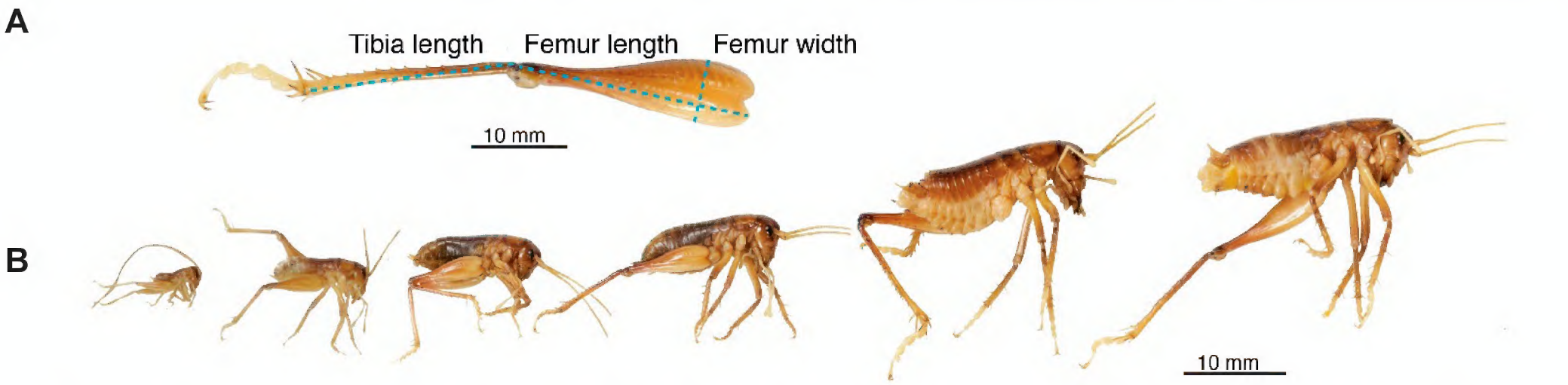

Fig. 3. *Hemiandrus* specimens collected from native forest at St Arnaud, New Zealand were used for size dimension analysis. **A.** Hind leg measurements used for size analysis are femur length, femur width, and tibia length. **B.** This is an example of the size range identified within a single species of *H. electra* males.

Results

This research aimed to understand the ecology of three *Hemiandrus* species that co-occur in the same forest. The study focused on understanding the dietary compositions, relative abundances, and sex ratios of the three sympatric *Hemiandrus* species, as well as the size distribution of the most common species (*H. electra*).

Diet of three sympatric wētā species.—All 66 specimens examined (male and female) contained food fragments identified as being of plant and invertebrate origin, although this differed in proportion among the species. Overall, crop content analysis showed that *H. nox* had fed significantly more on invertebrates than the other two species (Fig. 4). Approximately 80% of crop contents from *H. nox* were fragments from the remains of prey animals, whereas *H. electra* and *H.* 'disparalis' each had less than 20% of crop fragments identified as invertebrate. There was no significant difference between the diets of males and females in any of the three species ($p = 0.646$). Visual identification of the species of invertebrates and plants each fragment represented was not possible; however, the physical form was diverse. The invertebrate remains included antennae, exoskeletons, spider legs, cuticle of a caterpillar, and mandibles (Fig. 5). The plant fragments showed that these sympatric wētā species were polyphagous, as structures representing various plant types, including dicots and monocots, were observed (Fig. 6).

Relative abundance and sex ratio of the three sympatric Hemiandrus *species.*—A total of 966 wētā specimens were sorted from the malaise traps. Of these, 701 specimens were identified as *H. electra*, and 157 and 108 were identified as *H.* 'disparalis' and *H. nox*, respectively (Table 1). More individuals were trapped in January, February, and March (216, 268, and 170, respectively) than in November (56) and December (28). A higher abundance of males than females was observed during the study period (females = 419, males = 547). *Hemiandrus electra* had an almost equal sex ratio (355 males and 346 females), but males were more than twice as common in the traps as females for *H.* 'disparalis' (118 males and 39 females) and *H. nox* (74 males and 34 females). Ratios in March had the highest deviation from a 1:1 sex ratio, when 109 males were caught in the malaise traps but only 61 females (Table 1).

Size distribution of H. electra *females.*—The optimal number of clusters identified by Gaussian mixture models allowed each specimen to be classified into one of five groups, with 1 being the smallest and 5 being the largest individuals. These clusters may represent the different developmental growth stages (instars). Cluster 3 had the most abundant specimens, while cluster 1 had the fewest specimens (Table 2). Cluster classifications based on the three variables measured (tibia length, tibia width, and femur length) showed that the insects measured followed a linear growth pattern (Fig. 7). The first cluster consisted of the smallest instars (nymphs), while the largest specimens (cluster 5) were identified as adults. Individuals of *H. electra* for each of the five size clusters (putative instars) were caught in traps in each month, with the exception of cluster 1 (nymphs), which were absent in November (spring), December, and April (autumn; Fig. 8). Cluster 3 individuals were most abun-

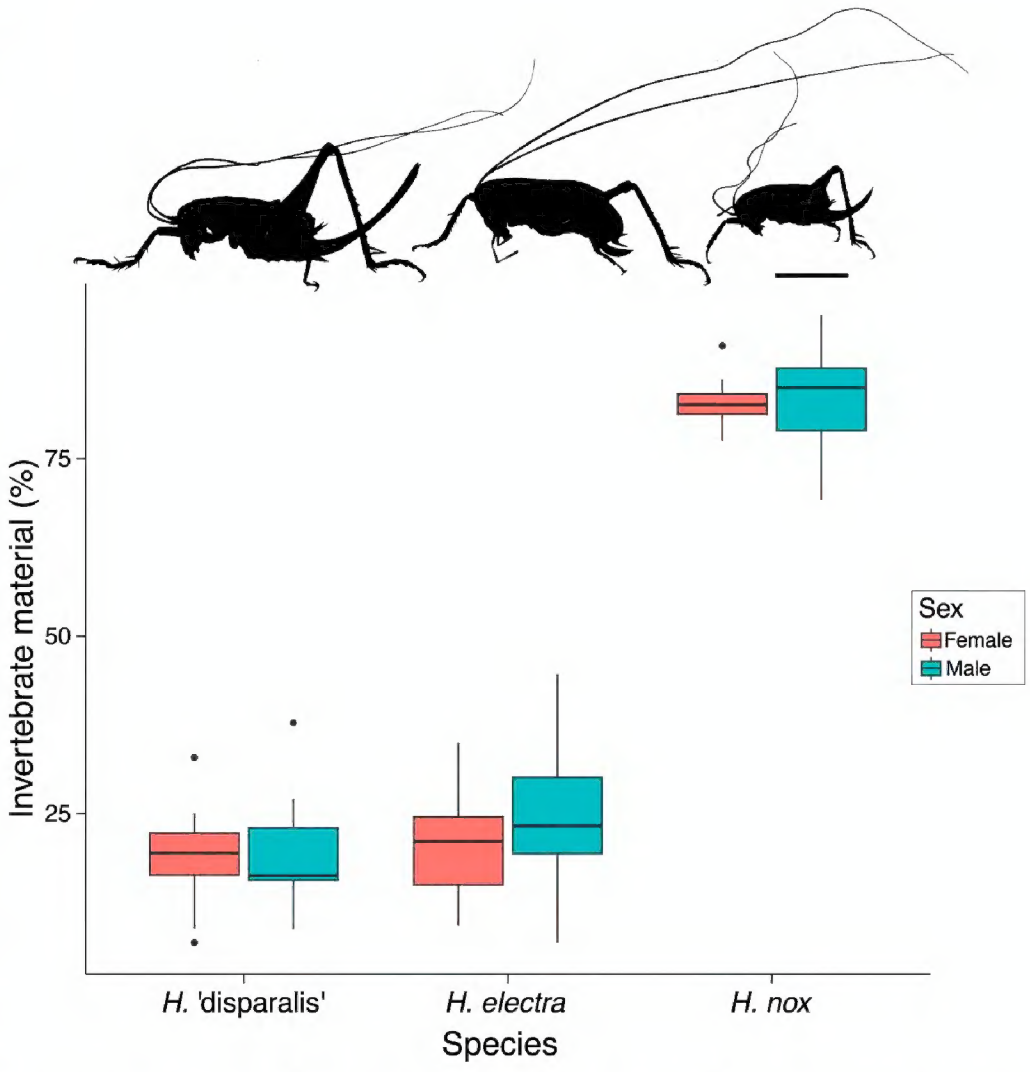

Fig. 4. Proportion (%) of food fragments in the crop of adult female (n = 11 for each species) and male (n = 11 for each species) wētā that derived from invertebrates. All other food particles in their diet were identified as of plant origin. *Hemiandrus* 'disparalis' (n = 22), *H. electra* (n = 22), and *H. nox* (n = 22) collected in malaise traps at the same time of the year in a native forest in St Arnaud, New Zealand (-41°53'59.99"S, 172°51'59.99"E). Data were analyzed for significant differences using a Tukey's (HSD) test at the 5% level. Error bars indicate the standard errors from a linear model.

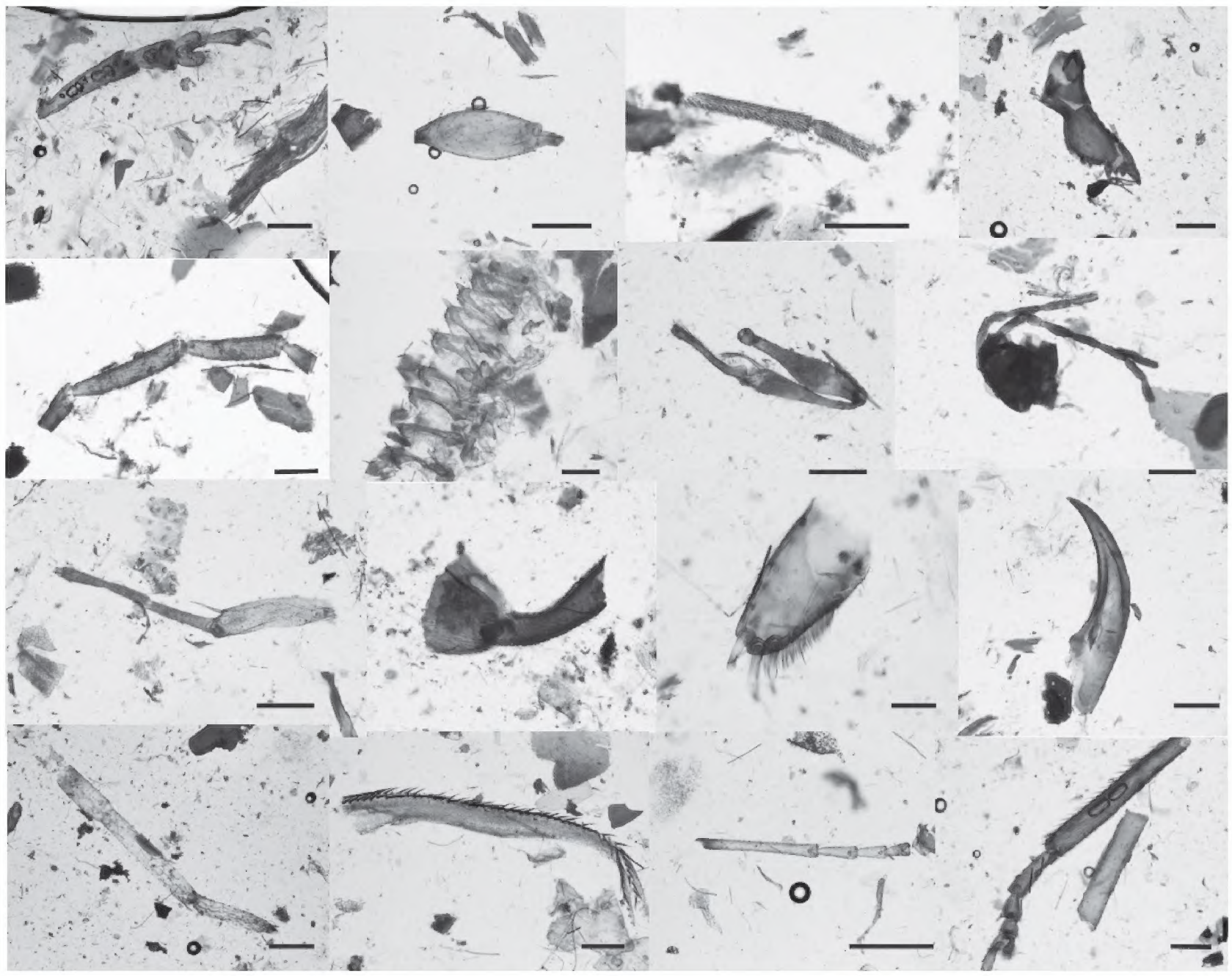

Fig. 5. Examples of food particles identified as invertebrate fragments, retrieved from the crop contents of three sympatric ground wētā species (*Hemiandrus*) caught in malaise traps from St Arnaud, New Zealand (-41°53'59.99"S, 172°51'59.99"E), native forest. Scale bar: 200 µm.

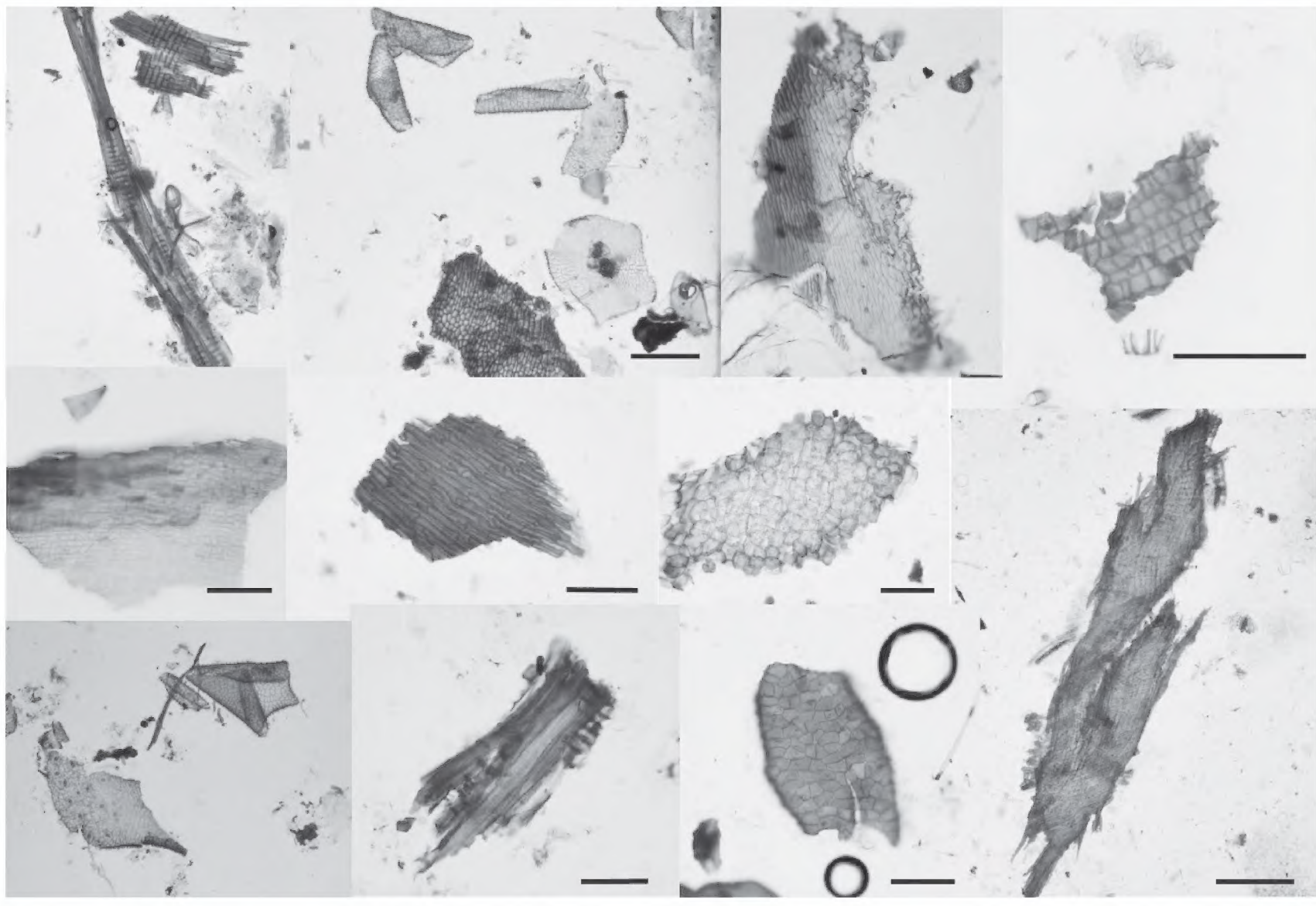

Fig. 6. Examples of food particles identified as plant fragments retrieved from the crop contents of three sympatric ground wētā species caught in malaise traps from St Arnaud, New Zealand (-41°53'59.99"S, 172°51'59.99"E), native forest. Scale bar: 200 µm.

Table 1. Abundance of three *Hemiandrus* wētā species caught in malaise traps in native forest in St Arnaud, New Zealand, and the number of each species and each sex in respective months of sampling. Data are combined for the 2004/2005 and 2005/2006 seasons.

Month	Season	Sex	*H.* 'disparalis'	*H. electra*	*H. nox*	Total
November	Spring	Female	0	25	5	30
November	Spring	Male	5	15	6	26
December	Summer	Female	2	12	5	19
December	Summer	Male	0	3	6	9
January	Summer	Female	12	90	8	111
January	Summer	Male	8	91	6	105
February	Summer	Female	2	99	8	109
February	Summer	Male	29	110	20	159
March	Autumn	Female	14	46	1	61
March	Autumn	Male	31	59	19	109
April	Autumn	Female	4	36	4	44
April	Autumn	Male	21	38	8	67
May	Autumn	Female	4	38	3	45
May	Autumn	Male	24	39	9	72
Total		**Female**	**39**	**346**	**34**	**419**
Total		**Male**	**118**	**355**	**74**	**547**
Grand Total		**Female + Male**	**157**	**701**	**109**	**966**

Table 2. The numbers of insect specimens in each size cluster identified using Gaussian mixture models with hind leg dimensions for *Hemiandrus electra* females caught in malaise traps in native forest in St Arnaud, New Zealand. Cluster 1 contains the smallest individuals, and cluster 5 contains adults.

Clusters	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Total
Number of specimens	29	52	142	67	56	**346**

dant in January and February (summer). Although adult *H. electra* (cluster 5) were uncommon in November, some were present in each month sampled (Fig. 8).

Discussion

New Zealand has a high diversity of nocturnal Orthoptera in the family Anostostomatidae. These insects are likely to be ecologically important in natural habitats (Griffin et al. 2011) and, in some modified areas, are recognized as horticultural pests (Nboyine et al. 2016, Trewick et al. 2021). However, there is still much to be learnt about their basic biology. This study obtained baseline ecological knowledge of three sympatric wētā species, *H. electra*, *H.* 'disparalis', and *H. nox*, about their diet, relative abundance, and life cycle patterns.

Diet of three sympatric Hemiandrus *species.*—Insects are categorized based on their dietary specializations, ranging from monophagous to polyphagous (Agrawal and Klein 2000). This study showed that *Hemiandrus* species feed on diverse plants (e.g., evidence of different plant epidermal cells, stoma, Fig. 6) and arthropod families (Fig. 5). Our observations are similar to those of other authors (Butts 1983, Van Wyngaarden 1995, Wahid 1979), confirming that ground wētā are omnivores. Diet proportions varied among the three sympatric *Hemiandrus* species studied. *Hemiandrus electra* and *H.* 'disparalis' fed more on plants than on invertebrates in contrast to *H. nox*. Various explanations have been offered for why omnivores select food species and quantities. Trade-offs probably exist between nutrient content, plant secondary metabolites, species abundance, physical traits, and opportunities. However, even at the coarse level of relative dietary components, we found that *H. nox* fed more on invertebrates, which accounted for up to approximately 80% of their diet. The diet of the closely related forest species *H. maculifrons* is almost entirely invertebrate (Cary 1983), similar to that of *H. nox*. A small

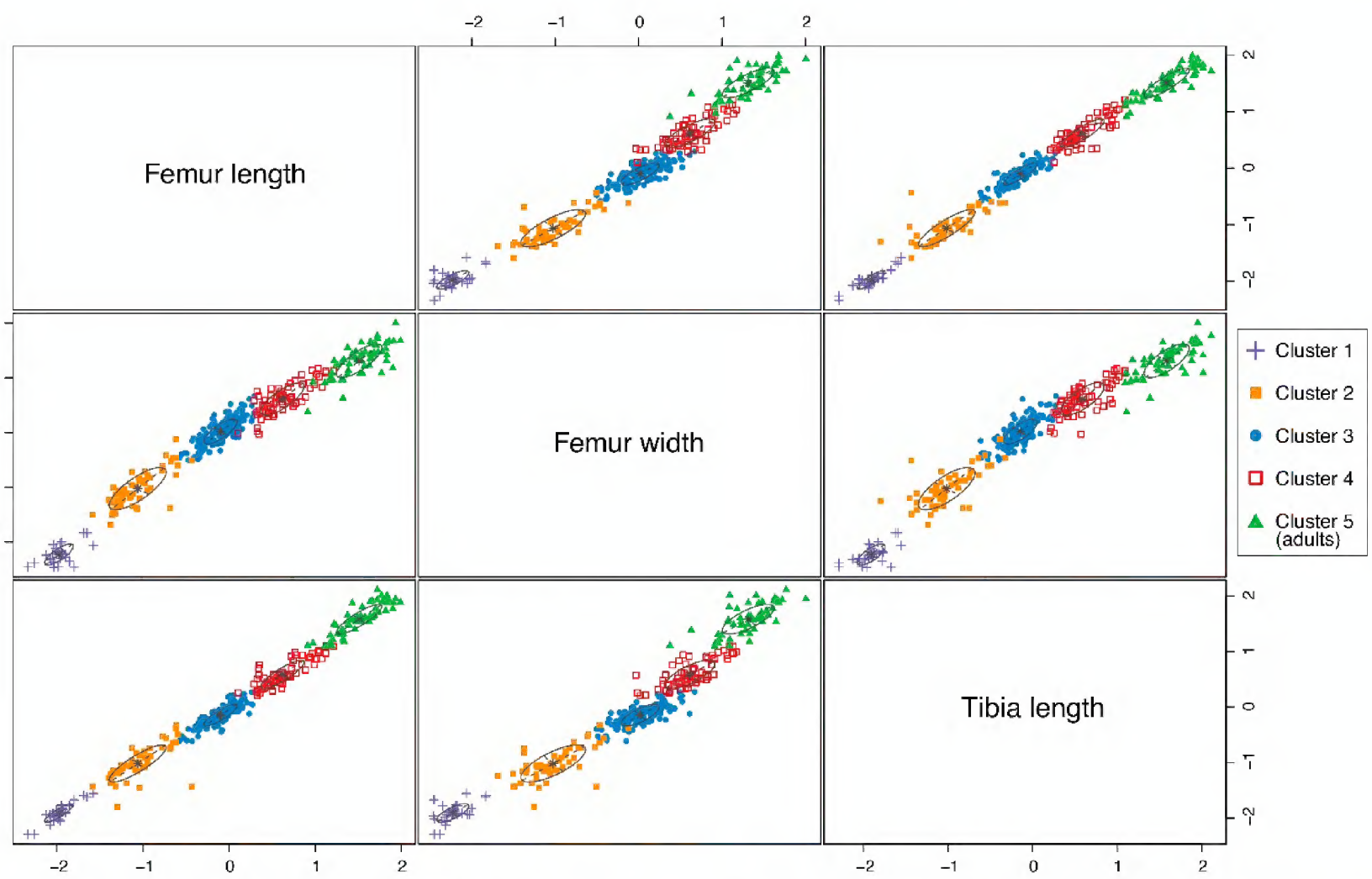

Fig. 7. Gaussian mixture models produced 5 cluster classifications using size of *Hemiandrus electra* female specimens collected over seven months (November–May) from malaise traps in native forest in St Arnaud, New Zealand. Models are based on tibia length, femur length, and femur width. (Purple = cluster 1, orange = cluster 2, blue = cluster 3, red = cluster 4 and green = cluster 5 (adults).

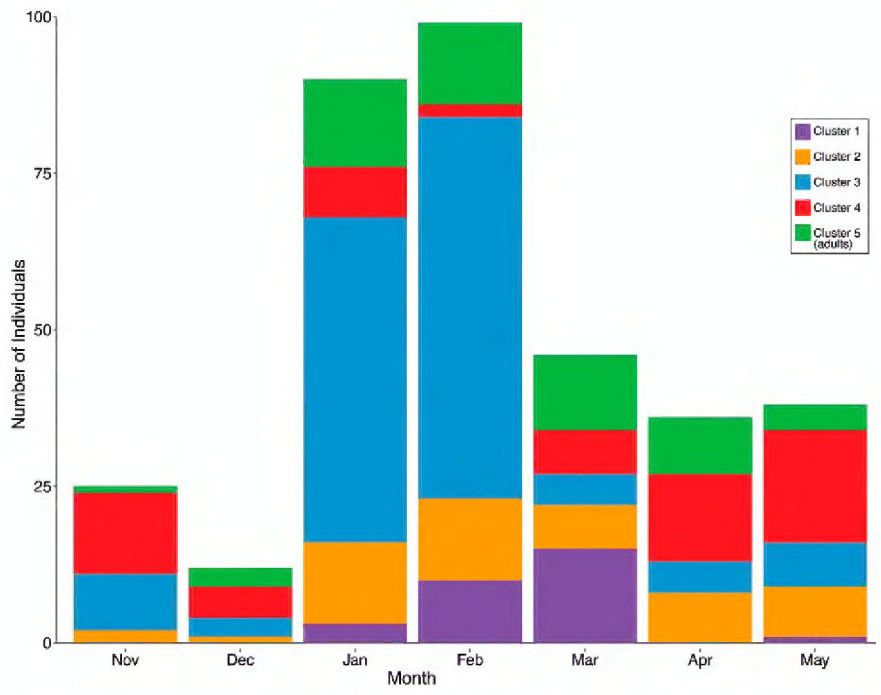

Fig. 8. Variation in size class abundance of female *Hemiandrus electra* collected over seven months (November–April) in malaise traps in native forest in St Arnaud, New Zealand (-41°53'59.99"S, 172°51'59.99"E). Size cluster classification using the Gaussian mixture model (n = 346).

proportion of the diet of *H. nox* was plant fragments (10–20%), which might be the result of preying on invertebrates with plant fragments in their guts (Cary 1983). During opportunistic night observations, many species of *Hemiandrus* have been seen scavenging (Cary 1983), but observing the hunting and capture of live prey would be much more challenging. The size of insect fragments in the crop could suggest that *H. nox* are scavengers, although *H. maculifrons* is considered an active predator (Cary 1983).

Unlike other studies of ground wētā that found differences in the diets of males and females (Wahid 1978), our study showed no diet differences between sexes at this coarse level, and these results are similar to observations of other species (Ramsay 1955, Richards 1953, 1962, 1973). This is unexpected, as males and females are often thought to have different nutrient requirements. For example, females are larger than males and require resources for egg production. However, males may also require more nutrients to present as nuptial gifts for females during mating, which may justify the similarities in the diets of these males and females (Gwynne 2004, Browne and Gwynne 2022). The current study investigated the dietary differences of adults and did not attempt to investigate the diet changes between successive instars. Most hemimetabolous insects do not show changes in diet between consecutive stages (Cary 1983). However, there is a possibility that adult *Hemiandrus* spp. feed on larger prey that they can subdue, while small instars may feed on smaller insects from Diptera and Diapriidae (Butts 1983, Cary 1983). Thus, further research on different life stages could reveal interesting dietary differences.

Relative abundance and sex ratio.—Three species of *Hemiandrus* were caught in the same malaise traps in a forest. We expected carnivorous species to be relatively less common than herbivorous species because, in general, biomass decreases for higher trophic levels in food webs. Although all three species had mixed diets (omnivores), the species with the highest proportion of invertebrates in its diet (*H. nox*) was the least common in the traps. However, as we intercepted only insects that climbed the malaise traps, it is possible the variation in abundance was the result of behavioral differences rather than relative population sizes in this forest habitat. Few data exist about the activity of *Hemiandrus* species in forests. However, we know that most species can be observed at night off the ground on foliage, and *H. pallitarsis* (Walker 1869) prefers to climb beech trees rather than other adjacent tree species (Moeed and Meads 1983). Very probably, behavior, size, reproductive strategy, diet, and other biological attributes can all be linked to the abundance variation of these three species, which may be phylogenetically constrained. However, the current study cannot determine the drivers of these differences.

Some previous studies of wētā in the family Anostostomatidae have found population samples to be either male- or female-biased; presumably, this is the result of using different survey methods. For example, stone wētā *Hemideina maori* (Joyce et al. 2004) and the tusk wētā *Motuweta riparia* (Gibbs 2002, McCartney et al. 2006) have been recorded as female-biased populations, while some studies of the ground wētā *Hemiandrus* found the sampled populations to be male-biased (Chappell et al. 2014). Sex ratio variation may be subject to data bias. Thus, factors such as sampling method and season must be considered. For example, during mating periods, ground wētā exit their burrows in search of mates, making 50:50 sex representations in traps likely during this period. After mating, females of some species with short ovipositors provide maternal care (*H. electra*, *H. bilobatus*) in their burrows. After mating, males exit their burrows in search of food and mates, while females are brooding. Thus, sampling during this period may show male-biased activity because females may rarely exit their burrows while caring for eggs and nymphs (Nboyine et al. 2016, Browne and Gwynne 2023). The sex ratio of the *Hemiandrus* species studied here and caught in the same malaise traps was biased in favor of males for *H.* 'disparalis' and *H. nox*, with male numbers double that of females (118:39 and 74:34, respectively). Surprisingly, the species with maternal care, *H. electra*, had equal numbers of males and females caught in traps in all seven months sampled (355:346).

Size distribution of H. electra *females.*—Several studies of wētā size distribution have suggested that the number of instars may range from 5 to 11, for example, 8 instars in *Hemiandrus celeano* (Wahid, 1979) and 10 or 11 in *Deinacrida fallai* Salmon, 1950 and *D. heteracantha* White 1842 (Richards 1973). Our Gaussian mixture model cluster classification of size measurements of *H. electra* females produced five size clusters of individuals. These five clusters might represent five instars. The adult specimens were all assigned to cluster 5, but the smallest specimens (cluster 1) might not represent first instar nymphs. Newly hatched (first instar) ground wētā might be too small to be trapped or to feed from the ground.

Our study found no evidence of seasonality in the growth and development of *H. electra* based on the population sample intercepted in malaise traps, as almost every size class was found in each month, with the absence of the most undersized individuals in November, December, and April. Similar to Leisnham et al.'s (2003) study of *H. maori*, we found that the smallest instars were most common from January to March. During this time, Leisnham et al. (2003) also observed gravid females in *H. maori*; this is presumable when wētā oviposit.

Conclusion

This study showed that ground wētā are omnivorous insects that feed on both plants and invertebrates. This knowledge is vital for understanding the ecology of wētā. Some wētā species have become pests of economic importance in crops such as grapevines. Thus, understanding the diet and plant species that wētā feed on in their natural habitats can help develop integrated pest management options with plant species mostly favored in natural habitats. We found that the three sympatric species of *Hemiandrus* vary

in abundance, with *H. electra* having the highest relative abundance when intercepted in malaise traps. Additionally, we found that females of *H.* 'disparalis' and *H. nox* were not caught as often as males, but *H. electra* had an even sex ratio of trapped specimens. This was somewhat surprising because *H. electra* is the only one of the three *Hemiandrus* species studied here with maternal care behavior. Thus, adult males were expected to be more common than adult females. Distinct sex ratios, diets, and abundance suggest that these three species are ecologically distinct. Given the ecological diversity we detected in sympatry, to understand the ecology of related *Hemiandrus* species, it is necessary to study populations in their natural habitats and not just extrapolate from related taxa.

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